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## THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA XX. SUMMARY

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ABSTRACT. A brief account is given of the geologic setting of the Triassic tetrapod faunas found in South America; the nature of the Chañares reptile fauna is summarized, and this fauna is compared with other Triassic assemblages in South America and other continents.

In nineteen previous papers in the Museum of Comparative Zoology *Breviora*<sup>1</sup>, an account has been published of the reptile fauna from the Triassic Chañares Formation of Argentina collected by the La Plata-Harvard expedition of 1964-65; this series includes, in addition to papers written by myself, contributions by C. Barry Cox, Farish A. Jenkins, Jr., James A. Jensen, and Arnold D. Lewis. Except for a future detailed study of the skull of the cynodont *Probainognathus* by Edgar F. Allin and myself I have no further plans for publication on the Chañares fauna. The present paper is intended to furnish a short summary of the results of the 1964-65 expedition. Except for a few forms recently described from the Chañares Formation, a recent paper by Bonaparte (1972) gives a succinct summary of all known reptiles from the South American Triassic, so that detailed references are unnecessary below.

As noted in previous papers in this series, I am deeply indebted to the National Science Foundation for grants for collection, preparation, and publication of the Chañares fauna.

### GEOLOGIC SETTING

Until the last few decades, almost nothing was known of the

<sup>1</sup>*Breviora* Nos. 247, 252, 264, 295, 333, 344, 352, 373, 377, 378, 379, 385, 389, 390, 394, 395, 396, 401, and 407.

Triassic tetrapod faunas of South America. Now, however, tetrapods are known from five discrete areas of Argentina and southern Brazil:

(1) The El Tranquilo Formation of Santa Cruz Province of Patagonia. From the upper part of this formation, obviously of Late Triassic age, have been collected prosauropod dinosaur remains. These have been studied by Casamiquela, but the results have not been published; they appear to pertain to the European genus *Plateosaurus*.

(2) The Puesto Viejo Formation, in southern Mendoza Province. Undescribed fragmentary remains are present in the lower part of the formation; from the upper part, Bonaparte has described a primitive but somewhat specialized traversodontid gomphodont *Pascualgnathus* and, most interestingly, forms indistinguishable from *Cynognathus* and *Kannemeyeria*, the most characteristic genera of the *Cynognathus* zone of the Upper Beaufort beds of South Africa. The Scythian age of this formation is obvious.

(3) The Cacheuta Basin. In the precordillera west of Mendoza is a series of beds of Triassic age, the Cacheuta Series. I have elsewhere (Romer, 1960) given a brief resumé of the geology. Four formations have long been recognized; in ascending order they are the Las Cabras, Potrerillos, Cacheuta and Río Blanco; recently a basal Río Mendoza Formation has been distinguished. Rusconi, in various publications (as Rusconi, 1951) has described vertebrates from these beds, including various fishes, many of uncertain systematic position, and from the Cacheuta Formation, flat-skulled amphibians of the genus *Pelorocephalus* [*Chigutisaurus*], which, although comparable in many regards to the brachyopids of other Gondwana continents, appears not to pertain to that group. Reptilian remains are rare; in the older collections there was, apart from a few scraps, only the postcranial skeleton of a primitive thecodont, *Cuyosuchus*. More recently an indeterminate jaw from the Potrerillos Formation has been described as *Colbertosaurus*, and Bonaparte has described the gomphodonts *Andescynodon* and *Rusconiodon* and a kannemeyeriid dicynodont, *Vinceria* from the Río Mendoza Formation. Because the flora of the Cacheuta Series is of the *Dicroidium* type present in the Late Triassic, Stipanovic (1969) believes the Cacheuta beds to be relatively Late Triassic in age. However since the *Dicroidium* flora extends well down toward the level of the Upper Beaufort beds of South Africa, Bonaparte's belief (1966, etc.) that part of the Cacheuta Series is

relatively Early Triassic in age is reasonable. Unfortunately the reptile fauna is as yet too fragmentary in nature for adequate comparisons to be made.

(4) Santa Maria Formation. From this Triassic formation in southern Brazil a few bones were early sent to the British Museum; major collections were later made by and for Huene, whose full results were published in 1944; further collections have been made by Price and White for Harvard University, by Colbert for the American Museum, and by Price for the Brazilian Geological Survey. The Santa Maria Formation has been described by Beltrão (1965) and by Bortoluzzi and Barbarena (1967). The vertebrate remains are confined to the upper part of the formation, and there is no known difference in the age of the beds between the three major collecting areas — near the city of Santa Maria, in the region of Chiniqua, west of that city, and in the Candelaria region, well to the east.

The fauna is varied, but the nature of preservation is such that structural details are frequently obscure and many forms are imperfectly known. Included are the procolophonid cotylosaur *Candelaria*; the rhynchosaur *Scaphonyx* [*Cephalonia*]; a number of thecodonts including *Cerritosaurus*, *Rauisuchus*, *Prestosuchus*, *Hoplitosuchus*, *Procerosuchus*; a fragmentary postcranial skeleton that appears to be a primitive saurischian, *Staurikosaurus* and a questionable second dinosaur, represented by a few vertebrae and limb bones; two carnivorous cynodonts, *Chiniquodon* and *Belesodon*; the gomphodont cynodonts *Traversodon* and *Gomphodontosuchus*; the dicynodonts *Barysoma*, *Dinodontosaurus* and *Stahleckeria*.

As discussed later, the Santa Maria Formation seems surely to be equivalent to the Los Rastros Formation of the Talampaya basin.

(5) The Talampaya basin or Villa Unión-Ischigualasto cuenca. This is the largest and most richly fossiliferous of the bone-bearing South American Triassic areas. It lies on the boundary between La Rioja and San Juan provinces, between the Sierra de Sañogasta on the east and the Ríos Bermejo and Guandacol on the west, and extends from the region of Villa Unión on the north to the Sierra de Valle Fertil on the south. Faults are numerous, but in general the Triassic beds can be grouped in two areas, east and west of the flat alluvium-covered Talampaya plain, the two areas being essentially the two limbs of a major syncline, with various formations present in reverse order on the two sides of the plain. The area to the west of the



plain is the better known and here the formations identified are much thicker than on the east: This region was explored by earlier geologists, but first adequately studied by Frenguelli (1946); his account has been modified and corrected by later workers, such as Groeber and Stipanovic (1953) and Ortíz (1968). To the northwest, in the region of Cerro Bolo there is an exceedingly thick series of beds that appear to extend continuously upward from the Carboniferous "Paganzo I" to the Late Triassic; this region was studied by de la Mota, whose work, unfortunately, remains unpublished. To the southwest the series, as far as published results are concerned, terminates below in the presumed Triassic "Paganzo III." For much of the western border this last is absent; if included, the major formations, in descending order, are:

Los Colorados Formation,  
Ischigualasto Formation,  
Los Rastros Formation,  
Tarjados Formation (= Paganzo III).

As described by Frenguelli, the Los Colorados beds were termed the Gualo Formation, a mistake corrected by Groeber and Stipanovic. The lower part of the Los Rastros Formation was synonymized by Frenguelli with the Ischichuca Formation; as pointed out by Ortíz this is incorrect, for the type Ischichuca, in the Cerro Bolo region, is synonymous with the main carbon-bearing beds of the Los Rastros. The lowest redbeds were thought by Frenguelli to represent the Permian "Paganzo II," whereas, as Ortíz states, they are the redbeds of "Paganzo III," or Tarjados.

Fragments of vertebrate skulls were recovered by Frenguelli from the Ischigualasto Formation and described by Cabrera in 1943. The richness of fossils in this formation was disclosed by the Harvard-Buenos Aires Museum expedition of 1958 (Romer, 1966). For many years, from 1958 on, the Ischigualasto beds were worked by expeditions from the Instituto Lillo of Tucumán, at first under O. A. Reig, later with great success by J. F. Bonaparte. The rich reptile fauna includes the rhynchosaur *Scaphonyx*; the thecodonts *Proterochampsia*, *Saurosuchus*, *Venaticosuchus*, *Triassolestes*, *Aetosauroides* and *Argentinosuchus*; the rare saurischian dinosaurs *Herrerasaurus* and (?) *Ischisaurus*; the ornithischian *Pisanosaurus*; fragmentary remains perhaps representing the carnivorous cynodont *Chiniquodon*; the gomphodonts *Exaeretodon*, *Proexaeretodon* and *Ischignathus*; the



dicynodont *Ischigualastia*. Except for representatives of *Ischigualasto* forms in transitional beds, no reptiles are known from the Los Rastros beds or the underlying Tarjados Formation. Above the Ischigualasto Valley rise the high cliffs of the Los Colorados. Except for a single dicynodont, *Jachaleria*, the faunal content of most of the thick series of Los Colorados redbeds is unknown; from the few meters available at the summit of the cliffs Bonaparte has described (1972b) a fauna of very late Triassic age, including the thecodonts *Riojasuchus*, *Pseudhesperosuchus* and *Neoaetosauroides*; the primitive crocodilian *Hemiprotosuchus*; the prosauropod *Riojasaurus*; and fragmentary materials comparable to *Tritylodon*.

We are here concerned mainly with beds lying to the eastern side of the basin, which was little studied by earlier workers; Jensen and I (1966) have discussed the geology here. Most of the formations present can be matched with those on the west side of the valley, although they appear to be much thinner here. The formations present (all adequately represented along the course of the Arroyo de Agua Escondida) are, in descending order:

- Los Colorados Formation,
- Ischigualasto Formation,
- Los Rastros Formation,
- Chañares Formation,
- Tarjados Formation,
- Talampaya Formation.

These formations are presumably underlain by the Carboniferous and Permian beds of "Paganzo I" and "Paganzo II," which are exposed on the slopes of the Sañogasta Range, east of a major north-south fault at the western margin of the mountains; in the area studied, however, we have not seen a contact between "Paganzo II" and the base of the Talampaya beds. The latter formation is best exposed in the cliffs forming the walls of the "Puerta de Talampaya," where 180–200 meters of these beds are present. They mainly consist of soft sandstones, but with occasional "cobbles." No fossils of any sort have been found. They appear to be purely continental in nature and are not improbably Early Triassic in age, or possibly Late Permian.

Unconformably above the Talampaya beds are the hard sandstones of the Tarjados Formation, some 385 meters in thickness at the Arroyo de Agua Escondida. These beds correspond, apparently, to part or all of the sandstones elsewhere termed

"Panganzo III." For the most part they are red, but in the southern part of the area studied the upper beds are white in color. Fossils are rare, but a few fragmentary dicynodont remains have been found in the upper layers. They are presumably Early Triassic in age.

On the irregular upper surface of the Tarjados sandstones lie unconformably the 75 meters of the volcanic ash deposits constituting the Chañares Formation. The uppermost layer of the Tarjados, about half a meter thick, forms an uneven, undulating surface of hard resistant materials suggesting hydrothermal action. Obviously there was major volcanic activity in the region at that time. The Chañares sediments show none of the layering that would be expected if the ash had been laid down in water; presumably there was merely a covering of the then existing surface with tremendous quantities of volcanic ash in Pompeii-like fashion. Bearing out such a conclusion is the fact that no trace of water-dwelling amphibians or fishes have been discovered in the Chañares and — more significant — almost all the numerous reptile remains found are in the lowest few meters of the ash deposits. Apparently the ash falls resulted in the local extermination of the vertebrate fauna.

As Jensen and I noted in 1966, it is not customary in Argentina to give a formation name to a set of beds of such limited thickness. I believe, however, that it is warranted in this case because of the distinctive nature of the sediments, and most especially, because of the vertebrate fauna contained in them.

Bonaparte (1967) suggested that the Chañares beds are equivalent to those of the Ischichuca Formation, the type section of which lies in the Cerro Bola region. However, both Ortíz (1968) and I (1971) have shown that this is incorrect. Bonaparte informs me that light-colored beds, which may be comparable to those of the Chañares, are present below the typical Los Rastros in the southwestern part of the basin, and that he has collected reptiles of Chañares type there. I have not visited this area. Ortíz includes these beds in the Los Rastros Formation, and if one does not wish to distinguish a separate Chañares Formation, one might include it in the Los Rastros — despite the marked contrast in the nature of the sediments — but could not, of course, consider these beds as part of the so-called "Ischichuca."

Conformably above the Chañares ash beds are the Los Rastros sediments of shales, clays, and sandstones, with intercalated carbonaceous layers, similar in nature to the beds of this forma-

tion in the western part of the basin. Because of numerous faults it is impossible to determine the thickness of the Los Rastros in this region, but it is obviously much less than the estimated 600 meters found west of the Ischigualasto Valley.

Only a limited exposure of Ischigualasto Formation sediments is present in this region; the thickness observed is but 175 meters, as compared with 400–500 meters in the type area. Above the Ischigualasto Formation are present Los Colorados beds, only 95 meters thick; whether this is the total amount originally deposited or whether they were originally thicker and later reduced by erosion before deposition of overlying Tertiary sediments is uncertain.

### THE CHAÑARES FAUNA

Below are listed the reptiles discovered in the 1964–65 expedition and described in earlier papers in this series. A few forms are represented by fairly complete specimens; others are known only from fragmentary materials. Much further collecting is possible; one may hope that if and when such collecting can be done, much better material of many of the forms already described may be obtained and additions be made to the faunal list:

#### Dicynodonts:

- Chanaria platyceps*
- Dinodontosaurus brevirostris*
- Dinodontosaurus platygnathus*
- Kannemeyeriid indet.

#### Gomphodont cynodonts:

- Massetognathus pascuali*
- Massetognathus teruggii*
- Massetognathus major*
- Megagomphodon oligodens*

#### Carnivorous cynodonts:

- Probelesodon lewisi*
- Probelesodon minor*
- Probainognathus jenseni*

#### Thecodonts:

- Luperosuchus fractus*
- Lagerpeton chanarensis*
- Lagosuchus talampayensis*
- Lagosuchus lilloensis*
- Chanaresuchus bonapartei*



*Gualosuchus reigi*

*Gracilisuchus stipanicicorum*

*Lewisuchus admixtus*

*Dicynodonts.* In contrast to the wealth of dicynodonts in the later Permian, the group in the typical Triassic deposits is restricted to a few forms of relatively large size (their place as herbivores appears to have been taken over mainly by rhynchosaurs and gomphodonts). In the Chañares beds such forms are present, but only in modest numbers, dicynodont specimens constituting but perhaps 5 percent or so of the total of reptiles collected. A few postcranial remains suggest the presence of a kannemeyeriid; apart from this, three types of dicynodonts are present, all of which are assigned by Cox to the characteristically Middle Triassic family Stahleckeriidae — *Chanaria platyceps*, *Dinodontosaurus platygnathus*, and *D. brevirostris*. *Chanaria* is a form not present elsewhere; however, the *Dinodontosaurus* species are quite similar to the genotypic form from the Santa Maria Formation (presumably of somewhat later age).

As also mentioned below, ecologic factors tend to separate stratigraphically and topographically the three common herbivore groups — dicynodonts, gomphodonts and rhynchosaurs — of the South American Middle Triassic fossiliferous areas. In the Santa Maria beds, dicynodonts and rhynchosaurs are, so to speak, “allergic” to one another; rhynchosaurs abound in the deposits near Santa Maria city but are unknown in the two other major fossil beds in this formation where dicynodonts are abundant. At Ischigualasto all known dicynodonts have been found in a stratigraphically narrow band, about half-way up the formation, and quite distinct from higher levels where gomphodonts abound, and from lower levels where rhynchosaurs are plentiful. In the Chañares beds, as noted above, almost all fossils are from the lowest part of the formation, but I have the impression that all dicynodonts collected were from the very base, within a meter or two of the unconformity with the Tarjados sandstones, whereas other types tended to occur up to a dozen or so meters higher.

*Gomphodonts.* Gomphodont cynodonts are the dominant herbivores in the Chañares beds; more than half of all specimens collected in the 1964–65 expedition were members of this group. Nearly all clearly pertain to a single genus, *Massetognathus*. In the first box of fossils received in Cambridge, Massachusetts, there was present a considerable series of specimens that seemed to sort out clearly into two size groups, and hence I described

them as belonging to two species, *M. pascuali* and *M. teruggii*. As I noted later, the full collection, when received, broke down such a clear distinction. Dr. James Hopson tells me that in primitive African cynodonts which he has been studying, a very considerable size range is to be found; this suggests that *M. pascuali* and *M. teruggii* merely represent populations of two sizes of the same species. However, as my tables show, the size distribution is heavily weighted above the peak that one may reasonably believe to represent mature adults, and the presence of two common species of *Massetognathus* is still a not unreasonable assumption. Still further, the size range of specimens that seem to belong to this genus is such that I find it impossible to believe that the amount of growth necessary to reach the size of the largest specimen can have been possible if a single species (or even two species) had been present, and hence have with some confidence given the name *Massetognathus major* to this relatively enormous skull.

Nearly all the gomphodonts in the collection appear to be reasonably assignable to a single genus. However, two rather large individuals are clearly distinctive, and I have given the name *Megagomphodon oligodens* to this rare form.

The Chañares gomphodonts are clearly members of the family Traversodontidae, a group to which all known South American gomphodonts belong (and also forms present in the Manda beds of East Africa). In the Santa Maria beds of Brazil gomphodonts are less common, and are represented mainly by the genus *Traversodon*. This genus may well have descended from *Massetognathus*, but its remains are too poor to allow a detailed comparison. The Ischigualasto traversodontids are obviously much more advanced types.

*Rhynchosaurs.* Quite as significant as the presence of certain forms in a given formation is the absence of expected types. Most Triassic reptile faunas, except those of the very earliest and very latest parts of the period, are notable for the presence of rhynchosaurs, often in great abundance. In our Chañares collections there is not the slightest trace of a rhynchosaur (despite the fact that identifiable elements of this type of animal, most especially upper tooth plates, are readily preserved and readily recognized).

Why are no rhynchosaurs present? It is not because they had not yet evolved, for although the Chañares beds date from a fairly early time in the Triassic, primitive rhynchosaurs were already present in the *Cynognathus* Zone, definitely earlier, and



were abundant in the Manda beds of East Africa, which (as discussed later) are probably somewhat earlier than the Chañares Formation. Quite certainly rhynchosaurs had evolved by the time of formation of the Chañares beds and (although there is no proof) may have been present in Argentina at that time.

Their absence here is quite surely, as I have suggested elsewhere (Romer, 1973), attributable to some ecologic factor. Rhynchosaurs and gomphodonts, in South American deposits at least, seem to be basically incompatible.<sup>1</sup> In the Ischigualasto beds, rhynchosaurs are exceedingly abundant in the lower part of the formation, but in our 1964–65 expedition we found no specimens in the upper half of the beds. On the other hand, on our expedition we found gomphodonts to be very rare in the lower part of the Ischigualasto Formation but very abundant in the upper half of these deposits. Rather surely the contrast is related to the type of plants present; the rhynchosaurs fed on some type of plants having a hard-shelled “seed” for which the “cracking” dentition of these forms was a necessity; the gomphodonts, as the grinding character of their teeth and the absence of a cracking device indicate, fed upon some different types of plant materials. In the Santa Maria Formation, gomphodonts are not as conspicuous as in the Ischigualasto and Chañares beds, but such gomphodonts as are present there are absent in the beds near Santa Maria city where rhynchosaurs alone are present. If, as is probable, rhynchosaurs were present in South America in Chañares times, they would presumably have been of a relatively primitive type, comparable to *Stenaulorhynchus* of the Manda beds rather than the more advanced genus present at Santa Maria and Ischigualasto.

*Carnivorous cynodonts.* In the Permian and earliest Triassic the typical carnivores are therapsids; during the Triassic carnivorous therapsids are reduced and disappear, to be replaced by archosaurs (but giving rise to the earliest mammals before disappearing completely). In the Chañares beds, thecodont archosaurs were becoming abundant, but carnivorous cynodonts were still present and modestly abundant. They are interesting in being more advanced than *Thrinaxodon* and *Galesaurus* of the earliest Triassic and without the somewhat specialized features seen in *Cynognathus*, the common form in the Late Beaufort of South Africa. *Probelesodon lewisi* is quite clearly ancestral to

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<sup>1</sup>Charig tells me, however, that there is no evidence for this in the Manda beds of East Africa.



*Belesodon* of the somewhat later Santa Maria beds; apparently two species are present, *P. lewisi*, fairly common, and a smaller form, *Probelesodon minor*. More interesting is *Probainognathus*, in which a startling advance is the presence of a socket — a glenoid cavity — in the squamosal for attachment of the jaw. This, however, is only a half-way stage in the development of the mammalian system of jaw suspension, for this glenoid is for the reception of an articular body of the lower jaw formed by a fusion of the posterior elements of the reptilian jaw type; the dentary bone, which in mammals articulates with the squamosal, is as yet not quite in touch with the squamosal. The teeth of *Probainognathus* are usually worn and show only the main fore-and-aft row of cusps present in the teeth of primitive mammals and seem to lack the row of basal “cusplets” found in early mammals. For this reason it was thought for a time that *Probainognathus* could not be on the direct line of ascent to mammals. However, Hopson has studied a little-worn dentition in which these cusps are present and hence it may be reasonably considered to be a true pre-mammal, or at least very close to the actual ancestral line.

*Thecodonts.* Although carnivorous cynodonts still survived, thecodonts were well on their way toward succeeding them as dominant carnivores. In earlier years we knew little of this group except for a few primitive forms in the Early Triassic and (apart from the specialized phytosaurs) only a few survivors in the Late Triassic, where the thecodonts were already being succeeded by the dinosaurs descended from them. One could have reasonably assumed that were Middle Triassic beds well known, the thecodonts would be discovered to be a varied group, with a variety of forms leading in different directions — toward pterosaurs, bird ancestors, crocodilians and dinosaurs. Our increased knowledge of Middle Triassic fossil deposits in recent decades has gone far toward verifying this assumption, for although many phyletic lines are far from clear, it is obvious that during the middle part of the Triassic the thecodonts were undergoing a rapid radiation into a wide diversity of types. The only large Chañares form is *Luperosuchus*, represented only by an incomplete skull, which appears to be a member of the prestosuchid (or rautisuchid) assemblage, of uncertain relationship. No close affinities are known for *Lewisuchus* or the two small long-legged types, *Lagosuchus* and *Lagerpeton*, represented mainly by hind legs. *Chanaresuchus* and *Gualosuchus* are long-snouted, probably amphibious forms related to *Cerritosaurus* of the Santa

Maria and *Proterochampsia* of Ischigualasto; once suggested as crocodilian ancestors, the proterochampsids do not seem to be related to that group, but are not impossibly related to the phytosaur pedigree. A progressive form is *Gracilisuchus*, related, it would appear, to *Ornithosuchus* of the later Triassic, which has suggestive resemblances to primitive theropods, although it is far from certain that the ornithosuchids are ancestral to these dinosaurs. The Chañares thecodonts, as was stated, increase considerably our knowledge of thecodont diversity, but as yet do little toward establishment of any major archosaur evolutionary lines.

### COMPARISON WITH OTHER FAUNAS

As knowledge of Middle Triassic faunas has increased, ideas as to the stratigraphic position and interrelations of these faunas have been expressed by a variety of workers, such as Bonaparte, Colbert, Cox, Reig, and myself. I shall here merely consider the interrelationships of these faunas from the point of view of the Chañares assemblage. I have recently reviewed the Triassic faunas in a plenary paper (1972) for the Second Gondwana Symposium, and hence full documentation here seems unnecessary.

As I pointed out some years ago (1966) Triassic faunas may be roughly divided into three successive groups, (A) early, (B) intermediate, and (C) late, although it is obvious that such distinctions cannot be completely clear-cut, and transitional assemblages may be expected. A-type faunas have long been known from the Upper Beaufort beds of South Africa, containing mainly therapsids, although with early members of other groups, notably thecodonts. C-type faunas are almost ubiquitous, being known from redbeds Late Triassic deposits in Europe, North America, South Africa, China, and (now) South America. In such faunas dinosaurs are already prominent, and their thecodont predecessors are still present, whereas therapsids are practically extinct (although the earliest mammals descended from them have now appeared).

As to B-type faunas, these were until recently almost entirely unknown, since deposits of Middle Triassic age in the northern continents are mainly marine, and in South Africa the Molteno beds, of Middle Triassic age, appear to be nearly barren of fossils (although footprints are abundant). What should one have expected in B-type faunas? Obviously, a transition between



A and C, with a gradual reduction of therapsids and an increase in archosaurs, including a variety of thecodonts and the beginnings of the dinosaurs. The B-type faunas now known from the southern continents do show these expected transitional features. But, in addition, they show positive characteristics of their own, in the great flourishing of gomphodont cynodonts and rhynchosaurs — groups that had their beginnings in the A-type faunas of the Early Triassic but seemed of little importance.

Let us first consider the South American situation. A-type faunas are certainly present in the Puesto Viejo Formation and not improbably in the Cacheuta series, as Bonaparte believes (although the evidence is still scanty). The C-type is present both in the upper part of the Los Colorados Formation, as now being developed by Bonaparte, and in the El Tranquilo Formation. Between, we have in Argentina the succession Chañares-Los Rastros-Ischigualasto, three formations that lie conformably one above the other in the Talampaya basin. The Los Rastros beds are almost barren of fossils, but it is, I think, generally agreed that the Santa Maria Formation of Brazil is equivalent, and thus, for vertebrates, our sequence may read Chañares-Santa Maria-Ischigualasto. All three clearly include B-type reptile faunas.

The Chañares beds, earliest of the three, clearly are an early part of the B complex. The gomphodonts are members of the traversodontid family, and the diademodontids and trirachodontid types present in the Scythian *Cynognathus* beds of South Africa appear to be extinct. The carnivorous cynodonts are of relatively advanced types — rather more advanced than *Cynognathus*. Rhynchosaurs are absent, but this, as noted above, appears to be due to some ecological factor, since primitive rhynchosaurs were already present in the A-type *Cynognathus* zone. And, while few thecodonts were present in the *Cynognathus* zone, they are here already varied in nature and in some cases at least, of a progressive type.

The Santa Maria beds are quite surely later in age than the Chañares beds but, just as the presumably equivalent Los Rastros beds lie in the break above the Chañares, the fauna of the Santa Maria beds follows that of the Chañares with some advances but without any major change. Among the dicynodonts, *Dinodontosaurus* continues little changed into the Santa Maria. Of gomphodonts, the Santa Maria *Traversodon*, although poorly known, may well be descended with little change from *Masetognathus*. The Santa Maria carnivorous cynodont *Belesodon*



appears to be but an enlarged edition of *Probelesodon* of the Chañares. In both Chañares and Santa Maria beds, most of the thecodonts are imperfectly known, but it is very probable that, given more adequate material, several close comparisons may come to be made, and *Cerritosaurus* of Santa Maria is very similar structurally to *Chanaresuchus* of the earlier formation. As Cox (1968) states, "the Chañares fauna is only slightly earlier than that of the Santa Maria." The only advance of any note is that here (as might be expected) we have the first sign of the evolution of dinosaurs from thecodonts in *Staurikosaurus* Colbert and possibly the fragmentary materials described by Huene as *Spondylosoma*.

Next above the Los Rastros Formation, without disconformity, lies the Ischigualasto Formation, from which a very considerable fauna is now known. The only dicynodont, *Ischigualastia*, is a large form of no particular stratigraphic significance. Gomphodonts of several genera — *Exaeretodon*, *Proexaeretodon*, *Ischignathus* — are exceedingly abundant, especially in the upper part of the formation. All are traversodonts that are more advanced than those of the Chañares and Santa Maria beds. Carnivorous cynodonts are rare and represented only by fragmentary remains that have been referred to the Santa Maria genus *Chiniquodon*. Thecodonts are, again, fairly common and varied. *Saurosuchus* is a relative of *Luperosuchus* of the Chañares but of larger size; *Proterochampsia* is similarly a large member of the *Chanaresuchus*-*Cerritosaurus* group. *Triassolestes*, originally thought to be a dinosaur, is probably a thecodont, but perhaps a crocodyloid relative. Interesting is the presence of *Aetosauroides*, first representative of a thecodont type that was to continue, apparently little changed, to Late Triassic times. Of dinosaurs we now have (although as rarities) the probable saurischians *Herrerasaurus* and *Ischisaurus* and, most interestingly, the oldest known ornithischian, *Pisanosaurus*. Despite advances, we have a close tie with the Santa Maria in that the common Ischigualasto rhynchosaur *Scaphonyx* (thoroughly studied in an unpublished thesis by Sill) is almost indistinguishable from the species present in the Santa Maria. Chatterjee (1969) has suggested that the Santa Maria localities containing *Scaphonyx* are later than those containing the remainder of the fauna. But there is no geological evidence to support this suggestion; all the vertebrate fossils, rhynchosaurs, dicynodonts and others, appear to come from the relatively thin upper portion of the Santa Maria Formation. In sum, the fauna of the Ischigualasto Formation

is advanced over that of the Santa Maria, but the difference is not great, as Bonaparte has noted.

We lack any means of correlation of these South American beds with the standard marine series, but since these faunas are obviously post-Scythian and pre-Norian, it is natural to suggest a one-to-one correlation of Chañares-Santa Maria-Ischigualsto with Anisian-Ladinian-Carnian. I have in the past expressed doubts as to whether the horizon of the Ischigualasto Formation was as high as the Carnian. In the European Keuper reptile remains are known only from the upper, Norian, part of the sequence and we have no knowledge of the reptile fauna of Carnian times. Further, in the Ischigualasto Valley the Los Colorados redbeds tower for some 400–500 meters above the top of the Ischigualasto beds and, except for a single dicynodont, our knowledge of the Los Colorados fauna is derived from the very topmost beds of this formation, so that it is possible that the lower part of these beds are of Carnian age. However, consideration of the faunas found in India and the northern continents (discussed below) suggests that our B-type faunas continued into Carnian days. It is thus very likely that the age of our B-type Middle Triassic faunas conflicts with the classic division of the Triassic into lower, middle and upper. Stratigraphically the Middle Triassic includes Anisian and Ladinian, while the Upper Triassic includes Carnian, Norian and Rhaetic; as regards vertebrates it is probable that the Middle Triassic includes Carnian and Anisian and Ladinian as well, with the “upper” C-type faunas restricted to the Norian and Rhaetic.

If one wishes to compare the Chañares and other South American B-type faunas with those of other continents, one naturally turns first to South Africa, since current theories of continental drift suggest that in the Triassic South America and Africa were closely apposed to one another. If this was the case one would expect similarities between the faunas of the two continents. But even if the South Atlantic were then nonexistent, there would remain a considerable distance between the Talampaya basin, and even the Santa Maria region, and the fossiliferous beds of east and south Africa. One should expect that there might be a considerable difference between the reptile faunas of these regions just as there is today a very considerable difference between the reptile faunas of, for example, California and the Atlantic coast areas of North America.

The African beds concerned are (1) the Molteno beds of the



Stormberg Series of South Africa, (2) the Ntawere beds of Zambia, and (3) the east African Manda beds.

The Molteno beds are quite surely Middle Triassic in age and should contain a fauna of the B-type. But while footprints are tantalizingly abundant, actual fossils are rare, and such few as have been described are of uncertain stratigraphic position and may either come from the top of the *Cynognathus* zone (as in the case of a cynognathid) or from the base of the redbeds (as in the case of a traversodont gomphodont).

The Ntawere beds are as yet not fully explored and as yet little material has been described (*cf.* Cox, 1969). Two zones appear to be present. The lower, in which *Diademodon* is present, may well be equivalent to the upper part of the *Cynognathus* zone, with an A-type fauna. The upper zone fauna includes two dicynodonts — the stahleckeriid *Zambiasaurus* and the kannemeyeriid *Sangusaurus*, two traversodont cynodonts, *Luangwa* and a second form as yet undescribed, and fragments of thecodonts. In default of fuller data, the age of this fauna is difficult to determine. The presence of traversodonts suggests the B-type; but traversodonts occur at an Early Triassic age in Argentina and may well have been as early in appearance in Africa.

Of especial interest is the Manda Formation of east Africa, from which a very considerable fauna is known, owing to collections made for Huene, by Parrington, and by an English expedition a decade ago. Unfortunately much of the known material is undescribed or described in only preliminary fashion. I am indebted to A. J. Charig for the faunal list given here. There are three dicynodonts, *Kannemeyeria*, *Tetragonias*, and a third undescribed form. No carnivorous cynodonts are as yet described, but gomphodonts are numerous and varied, including the diademodontids *Therapsodon* and (?) *Aleodon*, the trirachodontid *Cricodon* and a variety of traversodontids of which the only remains as yet described are assigned to four species of the genus *Scalenodon*. Some seven thecodonts have received names, including the prestosuchids *Mandasuchus* and (?) *Stagnosuchus*, and five further genera not assigned to families — *Parringtonia*, *Teleocrater*, *Hypselorhachis*, *Nyasasaurus* and *Pallisteria*. The abundant rhynchosaur remains pertain to the primitive genus *Stenaulorhynchus*.

The abundance of gomphodonts and rhynchosaurs indicates that we are dealing with a typical B-type fauna, and the presence of *Kannemeyeria* and of diademodontid and trirachodontid gomphodonts suggests a relatively early age. The fauna is ob-



viously earlier than that found at Ischigualasto, and the Santa Maria and Chañares faunas are the two South American assemblages with which comparisons might reasonably be made. On the whole, it is the Chañares fauna that seems to be the closest. The absence of rhynchosaurs in the Chañares beds removes one basis of comparison which might have been hoped for. Not improbably some of the Manda thecodonts will show affinities to Chañares genera when fully described. Crompton tells me that some of the Manda gomphodont specimens are closely comparable to *Massetognathus*, but here again we must await further publication. It is not unreasonable to expect that when the Manda fauna is fully described it will prove to be rather similar to that of the Chañares, but of a somewhat earlier date.

In more northern regions — India, Scotland and Nova Scotia — are assemblages that contain characteristic elements of the B-type fauna but are usually considered as of Late Triassic age. In the Maleri beds of India only three named tetrapods are present. These are: (1) a stereospondylous labyrinthodont generically identical with *Metoposaurus*, common in the Upper Triassic of both Europe and North America but otherwise unknown in presumed “Gondwana” areas; (2) a phytosaur, difficult to assign to a given genus (the systematics of phytosaurs are in a confused state) but representing a group unknown elsewhere in “Gondwana” areas except in Morocco; (3) a rhynchosaur *Parasuchus* [*Paradapedon*] of an advanced type which Chatterjee believes related to *Scaphonyx* of South America and *Hyperodapedon* of Elgin. The presence of a metoposaur and phytosaur in a supposed Gondwana region presents an interesting geologic problem, but the question of the age of the Maleri is almost equally interesting.

The Maleri is considered to be “Upper” Triassic; but while “upper” in a stratigraphic sense, it may well represent a Carnian fauna of our B-type. As regards phytosaurs, they are unknown in Europe before the Norian, but this group obviously had a long antecedent history (disregarding the question of the age of *Mesorhinus*). Metoposaurs, again, are “Upper” Triassic, but it is not improbable that there may have been older antecedent stages in the development of these peculiar stereospondylous labyrinthodonts.

Rhynchosaurs, in the form of the advanced genus *Hyperodapedon*, are present in the Elgin beds of Scotland, which Walker (1961) believes to be of Norian age. His conclusions

may be correct, and this may mean a late survival of rhynchosauroids in Europe. But it must be pointed out that there is no trace of a rhynchosauroid in the Norian Keuper of continental Europe, and hence it may be suggested that the Elgin beds are pre-Norian, perhaps Carnian in age. The Elgin fauna is a sparse one; there is nothing to represent the typical dinosaur fauna of the continental Norian (the systematic position of *Ornithosuchus* is questionable). Walker's correlation with the Norian is based mainly on the presence of *Stagonolepis*, a close relative of *Aetosaurus* of the continent. But we now know that the aetosaurid pattern was already present in the Ischigualasto beds in the form of *Aetosauroides* [*Argentinosuchus*], which is still incompletely known but appears to be a fully developed member of this group.

Most interesting is the report by Baird (1962 and *in litteris*) of the presence in beds in Nova Scotia which have been correlated with the Newark series of the Atlantic seaboard of the United States, of both of the most characteristic elements of the B-type fauna — rhynchosauroids and a gomphodont jaw! The Newark is a characteristically C-type series, as witnessed not so much by the rare dinosaurian fossil remains as by the vast numbers of dinosaur footprints. Are we dealing in these Nova Scotia finds with a very late survival of gomphodonts and rhynchosauroids? Or — more probably, I think — these supposed Newark equivalents in Nova Scotia may, in their lower beds, extend downward from Norian to Carnian age, into the time of existence of the B-faunas. Parenthetically, while the familiar red Triassic deposits of the western United States — Chinle, Dockum, Popo Agie — are usually considered as of quite Late Triassic age, we find in them mainly metoposauroid amphibians and phytosaurs, and little representation of the abundant dinosaurs found in the European Norian, the redbeds of South Africa, the Late Triassic of China and, apparently, in the Newark series proper. Is the nature of the faunas of these western beds associated with ecological factors or are they of pre-Norian age?

#### REFERENCES CITED

- BAIRD, D. 1962. Rhynchosauroids in the late Triassic of Nova Scotia. Geol. Soc. Amer. Spec. Paper, 73: 107.
- BELTRÃO, R. 1965. Paleontologia de Santa Maria e São Pedro do Sul, Rio Grande do Sul, Brasil. Bot. Inst. Cién Nat. Univ. Fed. Santa Maria, 2: 1-114.

- BONAPARTE, J. F. 1966. Chronological survey of the tetrapod-bearing Triassic of Argentina. *Breviora, Mus. Comp. Zool.*, No. 251: 1-13.
- . 1967. Comentario sobre la "Formacion Chañares" de la cuenca Triasica de Ischigualasto-Villa Unión (San Juan-La Rioja). *Acta Geol. Lilloana*, 9: 115-119.
- . 1972a. Annotated list of the South American Triassic tetrapods. *Proc. and Papers Second Gondwana Symposium (South Africa, 1970)*, Pretoria: 665-682.
- . 1972b. Los tetrapodos del sector superior de la formacion Los Colorados, La Rioja, Argentina. (Triásico Superior). I Parte. *Opera Lilloana*, XXIII: 1-183.
- BORTOLUZZI, C. A., AND M. C. BARBARENA. 1967. The Santa Maria beds in Rio Grande do Sul (Brazil). *Proc. Internat. Symp. on Gondwana Strat. and Paleont.*: 169-195.
- CABRERA, A. 1943. El primer hallazgo de terápsidos en Argentina. *Notas, Museo La Plata*, 8, Paleont., No. 55: 317-331.
- CHATTERJEE, S. 1969. Rhynchosauers in time and space. *Proc. Geol. Soc. London*, No. 1658: 203-208.
- COX, C. B. 1968. The Chañares (Argentina) Triassic reptile fauna. IV. The dicynodont fauna. *Breviora, Mus. Comp. Zool.*, No. 295: 1-27.
- . 1969. Two new dicynodonts from the Triassic Ntawere formation, Zambia. *Bull. Brit. Mus. (Nat. Hist.)*, Geol., 17: 255-294.
- FRENGUELLI, J. 1946. Consideraciones acerca de la "Serie de Paganzo" en las provincias de San Juan y La Rioja. *Rev. Mus. La Plata (N.S.)*, Geol., 2: 313-376.
- GROBER, P. F., AND P. N. STIPANICIC. 1953. Geografía de la Republica Argentina. Buenos Aires, II (Primera Parte): Triásico: 13-141.
- ORTÍZ, A. 1968. Los denominados estratos de Ischichuca como sección media de Formación Los Rastros. *Actas III Jorn. Geol. Argentina*, 1: 333-339.
- ROMER, A. S. 1960. Vertebrate-bearing continental Triassic strata in Mendoza region, Argentina. *Bull. Geol. Soc. Amer.*, 71: 1279-1294.
- . 1966. The Chañares (Argentina) Triassic reptile fauna. I. Introduction. *Breviora, Mus. Comp. Zool.*, No. 247: 1-14.
- . 1971. The Chañares (Argentina) Triassic reptile fauna. IX. The Chañares Formation. *Breviora, Mus. Comp. Zool.*, No. 377: 1-8.
- . 1972. Plenary paper. Tetrapod vertebrates and Gondwanaland. *Proc. and Papers, Second Gondwana Symposium (South Africa, 1970)*. Pretoria: 111-124.
- . 1973. Middle Triassic tetrapod faunas of South America. *Act. IV Congr. Latin. Zool. (Caracas, 1968)*, II: 1101-1117.
- , AND J. A. JENSEN. 1966. The Chañares (Argentina) Triassic reptile fauna. II. Sketch of the geology of the Rio Chañares-Rio Gualo region. *Breviora, Mus. Comp. Zool.*, No. 252: 1-20.



- RUSCONI, C. 1951. Laberintodontes Triásicos y Pérmicos de Mendoza. Rev. Mus. Hist. Nat. Mendoza, 5: 33-158.
- STIPANICIC, P. N. 1969. Las sucesiones Triásicas Argentinas. Gondwana Stratigraphy, I. U. G. S. Symposium (Buenos Aires, 1967): 1121-1150.
- WALKER, A. D. 1961. Triassic reptiles from the Elgin area: *Stiganiolepis*, *Dasygnathus* and their allies. Phil. Trans. Roy. Soc., London (B), 244: 103-204.